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# RHIZOPHORACEAE AND ANISOPHYLLEACEAE: SUMMARY STATEMENT, RELATIONSHIPS<sup>1</sup>

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## ABSTRACT

Each of Rhizophoraceae and Anisophylleaceae, as now defined by Tobe & Raven, are here considered to represent monophyletic units. Conspicuous autapomorphies of the variable Rhizophoraceae are, for example, the constellation of protein bodies of the sieve-tube plastids and the presence of colleter. Autapomorphies of the less variable and smaller Anisophylleaceae are sets of embryological, anatomical, and morphological characteristics as well as aluminium accumulation. The contributors of this symposium show convincingly from various fields how the two families differ in numerous details. These differences in combination support very strongly that the families are distinct from each other and are probably even rather distantly related. The Rhizophoraceae do not belong to Myrtales, from which they were excluded by all participants of a recent Myrtales symposium. Comparisons with various other groups show that Rhizophoraceae agree in many characters with especially Elaeocarpaceae, previously placed in Malvales, Celastraceae of Celastrales, and families of Geraniales, e.g., Erythroxylaceae, Humiriaceae, Linaceae, Lepidobotryaceae, and Oxalidaceae. This is supported in particular by a syndrome of embryological attributes, but also from morphological, anatomical, pollen morphological, and chemical evidence. Anisophylleaceae, which possess a combination of quite trivial character conditions, technically fit most closely with Rosales in the wide sense, i.e., Rosales–Cunoniales–Saxifragales, without approaching any particular family. Anisophylleaceae may have evolved from taxa related also to the ancestors of Myrtales.

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At a previous symposium held in Sydney (1982) the circumscription of the order Myrtales was critically considered. It was concluded (Raven, 1984) that two anatomical character states can be considered diagnostic features (“autapomorphies” in evolutionary terms) of this order: vestured pitting of the vessels and presence of intraxylary phloem. This implies that these character states were established in the ancestor of Myrtales.

At the Myrtales symposium (Raven, 1984) Thymelaeaceae and Rhizophoraceae were excluded with some misgivings from that order. Whereas the Thymelaeaceae possess the two above-mentioned anatomical characteristics (but show important differences from the Myrtales), the Rhizophoraceae lack them. The relationships of Thymelaeaceae as well as Rhizophoraceae have remained uncertain. The purpose of this symposium is to analyze and settle the relationships of the Rhizophoraceae.

Each of the families Thymelaeaceae and Rhizophoraceae, in their wide circumscriptions, con-

tains a group of somewhat erratic genera—the Gynostyloideae in Thymelaeaceae and the Anisophylleideae in Rhizophoraceae. When included, these elements amplify the variation in the two families and make difficult a proper evaluation of their affinities and evolutionary backgrounds.

The history of the systematic treatment of four genera, which are here assigned to Anisophylleaceae, has been outlined by Tobe & Raven (1987b; see also Juncosa & Tomlinson, this volume). Ridley (1922) was the first to acknowledge Anisophylleaceae as a family. Although genera of Anisophylleaceae have occasionally been referred to other families such as Euphorbiaceae, Olacaceae, and Saxifragaceae, they are usually considered closely related to the Rhizophoraceae, which is nearly always so for the Anisophylleaceae as a family.

The Rhizophoraceae have generally been placed in Myrtales, which is partly explained by the great similarity between the most well-known rhizophoraceous genera, *Rhizophora* and *Bruguiera*, with,

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for example, *Sonneratia*, which is a clear member of Myrtales. Previously, this genus and *Duabanga* made up the family Sonneratiaceae, but recent evidence shows that both are best placed separately in Lythraceae.

Looking aside from parallel mangrove adaptations, there remain a number of vegetative, floral, chemical, and pollen morphological similarities between Rhizophoraceae and Myrtales, which together have justified a position in or next to this order until the structures were more fully analyzed and the relationships carefully reconsidered in connection with the recent Myrtales symposium (see above). These similarities extend to habit, phyllotaxis, occurrence of leaf sclereids, floral construction (e.g., diplostemony), and some embryological details. In fact, the occurrence of intercolpate grooves ("pseudocolpi") on the pollen grains in genera (at least *Anopyxis*) of Rhizophoraceae (see Vezey et al., this volume) are surprisingly reminiscent of those in several families of Myrtales, although they must be explained as convergence or parallelism. A misleading psychological reason for considering Rhizophoraceae and Myrtales closely related may be that the colleters in Rhizophoraceae resemble the axillary, rudimentary stipule homologues in many Myrtales; however, well-developed stipules occur beside the colleters in Rhizophoraceae.

The Rhizophoraceae have also occasionally been placed in Loranthes (Dumortier, 1829) but more often in Cornales (as by Cronquist, 1968; Thorne, 1968). A position of Rhizophoraceae—or Anisophylleaceae—in Cornales is unjustified in view of the embryological and chemical pattern in that order, largely defined by unitegmic, tenuinucellate ovules and cellular endosperm formation combined with common occurrence of iridoid compounds (Dahlgren, 1975). The placement of Anisophylleaceae in Cornales by Dahlgren (1980a) was explained by the record at that time of unitegmic ovules in *Anisophyllea* (Karsten, 1891), but embryological conditions were otherwise largely unknown.

Airy Shaw (1966) claimed relationships between Rhizophoraceae and Combretaceae, Elaeocarpaceae, and Tiliaceae, and (in 1973) with Combretaceae, Rubiaceae, and Elaeocarpaceae. Combretaceae are clear members of the Myrtales; the possible relationships between Rhizophoraceae and these have been commented on above. Rubiaceae agree with Rhizophoraceae in having opposite leaves, interpetiolar stipules, and colleters, but in floral, chemical, and especially embryological characters, they are extremely different, ruling out a close relationship. More interesting is the mention

of Elaeocarpaceae. The similarity with this, for example in the lacinate petals, may first seem superficial, but other shared features (perhaps not considered by Airy Shaw), including some in embryology and chemistry, are worthy of careful consideration and will be evaluated below. Less obvious are the similarities between the Rhizophoraceae and the typically malvlean Tiliaceae.

In recent years, the Rhizophoraceae (without Anisophylleaceae) have sometimes been placed in an independent order, Rhizophorales, in either Rosidae (Cronquist, 1981) or in Myrtiflorae (Dahlgren, 1980a). The order Rhizophorales as established by van Tieghem & Constantin (1918) included Lecythidaceae in addition to Rhizophoraceae.

The position of the family Rhizophoraceae in any other order than its own has been regarded more or less unsatisfactory. Cronquist (1981) considered it, when placed in Myrtales, "as a giraffe in a herd of bison," and it is clearly out of place in both Cornales and Olacales.

Placing Rhizophoraceae in its own order solves no problem if our ambitions are to ally Rhizophoraceae with other groups of dicotyledons. It also remains to relate Anisophylleaceae with a family group and place it satisfactorily in an order.

When attempting to relate each of the Rhizophoraceae and Anisophylleaceae to other groups, the procedure has been to consider the variation pattern in each family in order to assess which character conditions can logically be regarded as relatively ancestral (plesiomorphic), that is, least advanced in the family, and which can be regarded as derived (apomorphic).

For the Anisophylleaceae, this poses no great problems, as the family is rather homogeneous. Tobe & Raven (1987b) have sketched the apomorphic conditions for the embryological features: unitegmic rather than bitegmic ovules; tapetal nuclei fused rather than not fused; a thin rather than thick seed coat; a base chromosome number  $x = 8$  rather than  $x = 7$ ; an *Allium*-type rather than *Polygonum*-type of embryo sac development; and unvascularized rather than vascularized integuments. These conclusions are based on common consensus and experience in evolutionary trends in dicotyledons and not on proper outgroup comparison, as is normally required in cladistic analyses. Actually, what we are still hunting is an acceptable outgroup of that family. In this case there is little controversy connected with the conclusions, but one can easily see risks in choosing which states are plesiomorphic first and concluding afterwards about an outgroup on the basis of biased opinions.

It is important that the choices of which features



are considered plesiomorphic in a family are soundly based, since the plesiomorphic and not the apomorphic states decide the conclusions as regards relationships to other families, whereas the apomorphic states and not the plesiomorphic must govern the conclusions on evolution within the family.

Risks for biased opinions become more obvious when dealing with the much more variable Rhizophoraceae. Here, the logical step has been to regard the mangrove genera, the tribe Rhizophoraceae, as secondarily adapted in a number of characters ranging over vegetative and reproductive structures, a view for which Juncosa & Tomlinson (this volume) give ample evidence.

We are thus left mainly with the other tribes in Rhizophoraceae for conclusions on outward relationships, although presumably various chemical, anatomical, and embryological character states of tribe Rhizophoreae may have retained features of ancestral Rhizophoraceae, such as perhaps peculiar sieve-tube plastid inclusions, features of flavonoid and alkaloid chemistry, and presence of colleters, endosperm, and endothelium. Thus, emphasis is first laid on character states shared among all the tribes of the family, then on states common to tribes Macarisieae, Hypogyneae, and Gynotrocheae, or at least to some members in each of these tribes.

In my contribution I have disregarded completely the alignments between each of Rhizophoraceae and Anisophylleaceae and other groups in current systems of classification. I have compared character conditions of the kind just mentioned with those in various conceivably related families. It turned out that the current classifications help little in indicating groups with profound and all-around similarity to each of the two families.

Contrary to what was first expected, it has been much easier to suggest relationships for the larger and more variable Rhizophoraceae than for the small, more homogeneous Anisophylleaceae. This depends on the fact that Rhizophoraceae possess a number of rather unusual, presumably advanced attributes, such as a peculiar combination of embryological character states matched only in a few other families, peculiar alkaloid chemistry, and a characteristic seed coat. Luckily enough, the collective evidence all points in the same direction: toward a few families rarely or never considered previously as close relatives of Rhizophoraceae. Even though some of the similarities used in the forthcoming arguments are likely to be caused by convergent evolution, all are not likely to be so. According to the conclusions, the Rhizophoraceae are considered to be most closely related to families

previously referred to three different orders, Malvales, Celastrales, and Geraniales, leading to a completely new view of their positions in the dicotyledons.

For Anisophylleaceae, the conditions are less favorable, since nearly all character states in which they differ from the Rhizophoraceae represent frequent states, some of them presumably less derived than the corresponding ones in Rhizophoraceae, giving fewer clues to the closest relationships.

Within some orders and superorders certain families possess many plesiomorphic character conditions, making them rather similar and difficult to place. Thus, a combination of various trivial character conditions, such as in Anisophylleaceae, with small to medium-sized, tetramerous, heterochlamydous, choripetalous, diplostemonous, and isomerous flowers, gives little guidance to any particular relationships.

#### CHARACTERIZATION OF RHIZOPHORACEAE

The Rhizophoraceae comprise a variable group of genera divisible into three tribes after the following model:

Tribus **MACARISIEAE**: *Anopyxis* (Pierre) Engl. (3 species); *Blepharistemma* Wall. ex Benth. (1 species); *Cassipourea* Aubl. (55 species); *Dactylopetalum* Benth. (15 species, if distinct from *Cassipourea*); *Comiphyton* J. J. Floret (1 species); *Macarisia* Thouars. (7 species); and *Sterigmopetalum* Kuhl. (7 species).

Tribus **GYNOTROCHEAE**: *Carallia* Roxb. (9 species); *Crossostylis* J. R. & G. Forst. (10 species); *Gynotroches* Bl. (1–4 species); and *Pellacalyx* Korth. (8 species).

Tribus **RHIZOPHOREAE**: *Bruguiera* Lam. (6 species); *Ceriops* Arn. (2 species); *Kandelia* W. & A. (1 species); and *Rhizophora* L. (8 species).

The difficulty in defining the family by gross morphology is reflected in the fact that it comes out in 17 different places in the revised Thonner key (Geesink et al., 1981), although in this key Anisophylleaceae are included in Rhizophoraceae and account for four of these places.

Differences from the Anisophylleaceae are the opposite leaves and the interpetiolar stipules.

The most characteristic feature of Rhizophoraceae is perhaps the unusual type of sieve-tube plastids: with ca. 20 or more square to polygonal protein bodies of variable size (0.1–0.5  $\mu\text{m}$ ) (Behnke,



this volume). These were found in *Bruguiera*, *Carallia*, *Crossostylis*, *Rhizophora* (Behnke, 1982), *Cassipourea*, *Ceriops*, *Kandelia*, and *Sterigma-petalum* (Behnke, 1984). Sieve-tube plastids of this type are known only in two more families: Erythroxyloaceae and Cyrillaceae, both with somewhat fewer protein bodies, and the last family also with protein filaments in the plastids (Behnke, 1982). This character state represents a significant autapomorphy of the Rhizophoraceae. In Anisophylleaceae the sieve-tube plastids possess starch grains only (Behnke, 1982, 1984).

Another unusual feature, an autapomorphy found in both mangrove and nonmangrove genera of Rhizophoraceae, is the presence of colleters at the leaf bases (Hou, 1958, 1960). Lersten & Curtis (1974) described their construction in *Rhizophora mangle*.

These characters, especially when supplemented with some embryological features mentioned below—for instance, the combination of bitegmic crassinucellate ovules with integumentary tapetum (endothelium)—may suffice as arguments for considering Rhizophoraceae as a monophyletic unit, which could otherwise be doubted from the rich variation in vegetative, floral, wood anatomical, and other characters.

According to Keating & Randrianasolo (this volume), the leaves have brochidodromous or eucamptodromous venation. Lateral teeth are associated with mainly the latter kind of venation and are found in less coriaceous leaves of certain nonmangrove taxa, mainly in the tribe Macarisieae; they are called “macarisioid teeth.” Whether occurrence of teeth represents a plesiomorphic or apomorphic state is uncertain, and perhaps no phylogenetic conclusions can be based on them. Stomata are confined to the lower surface of the leaves; the brachyparacytic type is most widespread in the family; and this was possibly the plesiomorphic state. Cyclocytic stomata are found in the Rhizophoreae and appear to represent a derived type in the family. It is interesting that prismatic crystals and crystal druses occur in Rhizophoraceae but are largely vicarious: prismatic crystals being found in the Macarisieae, where crystal druses are very rare (confined to *Blepharistemma*), while all other genera only have crystal druses. Thus crystals help with tribal division within the family. Laticifers, often articulated, are common in some species (Keating, 1984).

According to van Vliet (1976), the wood anatomy of the Rhizophoraceae is highly variable. The perforation plates of the vessels are usually sca-

lariform, with 5–87 perforations. In this the Rhizophoraceae differ from the Anisophylleaceae, which have simple perforation plates. The vessel diameter in Rhizophoraceae is also typically smaller than in Anisophylleaceae. Furthermore, intervessel pits are alternate in Anisophylleaceae but opposite in most Rhizophoraceae. Within Rhizophoraceae, it is the tribe Gynotrocheae that approaches most the Anisophylleaceae, and within that tribe particularly the genus *Carallia*, in which vessel perforation may even be simple.

The inflorescences of Rhizophoraceae are generally few- to several-flowered cymes, or the flowers may also be simple. The inflorescences are situated in leaf axils.

Rhizophoraceous flowers vary from hypogynous to epigynous. They are, for example, hypogynous in Macarisieae, for some genera of which a particular tribe, Hypogyneae, has been proposed. Other genera have more or less perigynous, half-epigynous, or epigynous flowers. The hypogynous (or possibly somewhat perigynous) condition is likely to be plesiomorphic.

According to Juncosa & Tomlinson (this volume) Rhizophoraceae exhibit subepidermal floral laticifers of two tribally distinctive types. The numbers of sepals and petals each vary between 4 (as in *Rhizophora*) and 16 (in *Bruguiera*). The sepals are valvate. The sepal traces are of the split-lateral type (Juncosa, unpubl.). Apically lacinate petals are common in the nonmangrove genera. Among these, especially in *Cassipourea*, the petals recall the lacinate petals in certain genera of Elaeocarpaceae (Arena & Orsini, 1973). Fringed petals also occur in Anisophylleaceae and may represent the main reason why the genera of this group have so readily been included previously in Rhizophoraceae.

Interestingly, in the tribe Rhizophoreae the petals do not form a whorl, but each individual petal encloses one or more stamens opposite it. Juncosa & Tomlinson (1987) regarded this as an autapomorphy of this tribe. Stamens with a narrow filament and a well-defined truncate, tetralocular anther, as found in most nonmangrove genera, probably represent the plesiomorphic state, whereas the more specialized types of mangrove genera are derived. Tomlinson et al. (1979) showed that pollen is often released explosively, and pollen dispersal is highly variable: by wind, flies, other small insects, butterflies, night-flying moths, or even birds.

It is assumed that the plesiomorphic androecial condition for Rhizophoraceae is the diplostemonous, but many more stamens occur in some gen-



era, e.g., about six times the petal number in *Kandelia* (Juncosa & Tomlinson, 1987). In *Ceriops tagal*, at least, all stamens belong to one whorl and arise on a ring primordium, whereas in *Bruguiera* two whorls of stamen initials are formed. This was used as evidence by Juncosa & Tomlinson (1987) that the remarkable explosive pollen discharge mechanism is derived independently in the two groups. The multistaminal condition is here regarded as derived by increase in number of initials. This is a common phenomenon in Myrtales, where increased stamen number has evolved in several families independently, and, for example, in Lythraceae obviously a few times.

Pollen grains of Rhizophoraceae according to Vezey et al. (this volume) are 3(-4)-colporate, and their exine has a rugulate-punctate (to psilate) surface. (The exine is proportionally thicker than that in Anisophylleaceae, where the surface sculpture is reticulate-punctate.) Vezey et al. (this volume) report "subsidiary colpi" or "pseudocolpi" on the pollen grains in some members of the tribe Macarisieae, this being a conspicuous similarity to the conditions in many Myrtales. The pollen grains in Rhizophoraceae are dispersed in the two-cellular stage.

The pistil is usually surrounded by a fleshy, often conspicuously lobate disc (said by Hou, 1958, to be lacking in *Pellacalyx*). The base of the stamens may be variably attached to this disc (Hou, 1968).

The pistil generally has a 2-12-locular ovary, each locule with from two to rather numerous (in *Pellacalyx* to ca. 25) ovules on an axile placenta. *Kandelia* is, however, an exception from this; its ovary is unilocular and contains about six apically inserted ovules.

The style is simple or slightly branched apically, as in *Gynotroches*; the latter state may be the most ancestral in the family. The stigma is terminal and capitate or more or less lobate; in *Gynotroches* the apical stylar branches are stigmatic. (The simple style contrasts to the separate stylodia in Anisophylleaceae.)

The embryological conditions in Rhizophoraceae (see, for example, Karsten, 1891; Cook, 1907; Mauritzon, 1938; and Juncosa, 1982, 1984a, b) are as follows. The ovules are anatropous or hemitropous, bitegmic, and crassinucellate, although sometimes rather weakly crassinucellate. The inner integument is three- to multilayered, and the outer two- to multilayered, depending on genus and stage of the ovule. The micropyle is at least usually zigzag. A parietal cell is always cut off from the primary archesporial cell and divides a number of

times to form a modest parietal tissue. Embryo sac development, as far as known, is of the *Polygonum*-type. Endosperm formation is nuclear. During embryo sac development and the early stages of endosperm formation, the nucellar tissue lateral to the embryo sac disintegrates, so that this comes to border upon the inner integument. The inner layer of this develops an endothelium in at least several genera. The seeds are endospermous. The cells of the outermost layer of the inner integument (the exotegmen) become elongate and fibrous in most genera (comprising "Legnotidaceae" in Corner, 1976), although this is not the case with the genera of the tribe Rhizophoreae nor in *Carallia* of Gynotrocheae; see Juncosa, 1984a).

An aril is present in at least four genera of the tribe Macarisieae, e.g., *Cassipourea* (Schimper, 1892) and *Comiphyton* (Floret, 1974; Tobe, pers. comm.). This aril represents an expansion from the micropylar part of the outer integument, i.e., it is *exostomal*.

The fruits are normally capsular, dry or fleshy, although nonclassifiable in the viviparous genera. They are sometimes stated to be indehiscent. Frequently they do not have more than one seed per locule, sometimes only one seed altogether. The seeds (see above) have a chlorophyllous embryo (Schimper, 1892). The embryo has two well-developed cotyledons in the nonmangrove genera; in *Bruguiera* there are 2-4 cotyledons according to Schimper (1892); in *Rhizophora*, *Kandelia*, and *Ceriops* the cotyledons are fused into a handweight-shaped structure. In the mangrove genera the embryo grows continuously and the seed has no resting period, a condition called "vivipary." Vivipary and specializations connected with this are secondary adaptations.

The basic chromosome number according to Raven (1975) is  $x = 18$  and  $x = 32$ .

Chemically, the Rhizophoraceae can be classified as tannin plants. Bark of some genera has up to 40% or more of condensed-type tannins (for references, see Hegnauer, 1973). Ellagic acid has rarely been detected, and then in low quantities (in *Cassipourea*). Both caffeic acid and proanthocyanin are present. Of flavonoid compounds, also kaempferol, quercetin, myricetin, leucodelphinidin, and leucocyanin are recorded within the family (Hegnauer, 1973).

Alkaloid chemistry in Rhizophoraceae is possibly important and will be further discussed below. Derivatives of tropane, pyrrolizidin, and hygrolin bases have been detected in different genera and, according to Hegnauer (1973), are probably all



TABLE 1. *Features judged to be primitive (plesiomorphic) in Rhizophoraceae sensu stricto.*

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Sieve-tube plastids with several to numerous, square to polygonal protein bodies
Vessels with scalariform perforation plates
Intervessel pitting opposite
Laticifers probably present
Leaves opposite
Leaf venation at least partly brochidodromous
Stomata brachy-paracytic on lower surface of leaves
Prismatic oxalate crystals present (possibly also crystal druses)
Colleters at leaf bases
Inflorescences multiflorous cymes or cymules
Flowers hypogynous, probably pentamerous, diplostemonous
Disc present, prominent
Petals probably apically laciniate
Stamens with narrow filaments
Anthers well defined, $\pm$ ovate, tetralocular, with longitudinal dehiscence; insect pollination
Pollen grains tricolporate, with rugulate-punctate surface; without pseudocolpi(?)
Perhaps style simple, apically five-brachiate
Ovary with five locules
Ovules probably two per locule, axile
Ovules anatropous, bitegmic, crassinucellate, with three- to several-layered inner integument
Endothelium present
Seed coat exotegminal, with "fibrous" cells
Aril probably present, formed from the apex of the outer integument (exostomal)
Fruit capsular
Embryo chlorophyllous, with well-developed cotyledons
Alkaloids formed from the amino acid ornithine present

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derived from ornithine. Some of the alkaloids are sulphated (Ettlinger & Kjaer, 1968). Rhizophoraceae (contrary to Anisophylleaceae) do not show aluminium accumulation. The endosperm of the seeds is nonstarchy and contains fatty oils.

The above evidence, in combination with the pantropical distribution pattern with Old World concentration, will form the basis for the following comparative remarks.

#### "RHIZOPHORACEOUS" CHARACTER CONDITIONS IN OTHER FAMILIES

##### METHODOLOGY

In the search for one or more families that are closely related to Rhizophoraceae it is essential to consider the character conditions judged to be plesiomorphic in Rhizophoraceae. These states have been indicated for a number of characters above.

The characters that should be most successful in the search for closely related families will simultaneously fulfill the following qualifications:

1. Character states that occur in most or all Rhizophoraceae or at least in a fair variety of the nonmangrove genera; these states are likely to be *plesiomorphic in Rhizophoraceae*.
2. Character states that are likely to be *apomorphic in a larger assemblage*, such as in a superorder; i.e., *character conditions that are not archaic in dicotyledons*.
3. Character states that are rather *unusual in dicotyledons at large*, or *have a defined distribution among them*.

Briefly expressed, we must first search for more or less advanced character states that are likely to have been established in an ancestor of a group of families that includes Rhizophoraceae.

Beyond individual peculiar character states present in Rhizophoraceae, *combinations* of character states should be considered, because unusual combinations are not likely to have evolved in different evolutionary lines. Exceptions are such combinations of character states that have evolved in response to a defined, extreme environmental pressure favoring special syndromes. Therefore, the mangrove genera, which are specialized in numerous respects and show multiple similarity to other mangrove genera, are unsuitable for comparison. It is true that also rainforest habitats favor certain morphs, but these are presumably less specialized than the mangrove ones.

Character conditions evaluated here include the following:

1. Presence of endothelium.
2. Presence of aril.
3. Exotegmic seed coat.
4. Chlorophyllous embryo.
5. Sieve-tube plastids with the protein bodies typical of Rhizophoraceae.
6. Presence of certain types of alkaloids.
7. Combined occurrences of the above (and other features).

Families found to share with Rhizophoraceae the unusual character conditions mentioned above will be compared further with Rhizophoraceae with regard to more general characters. If these turn out to be greatly divergent, the selected character conditions mentioned above are likely to reflect convergence rather than close relationship. If, however, a family shows similarity with Rhizophoraceae both in these selected characters and overall prop-



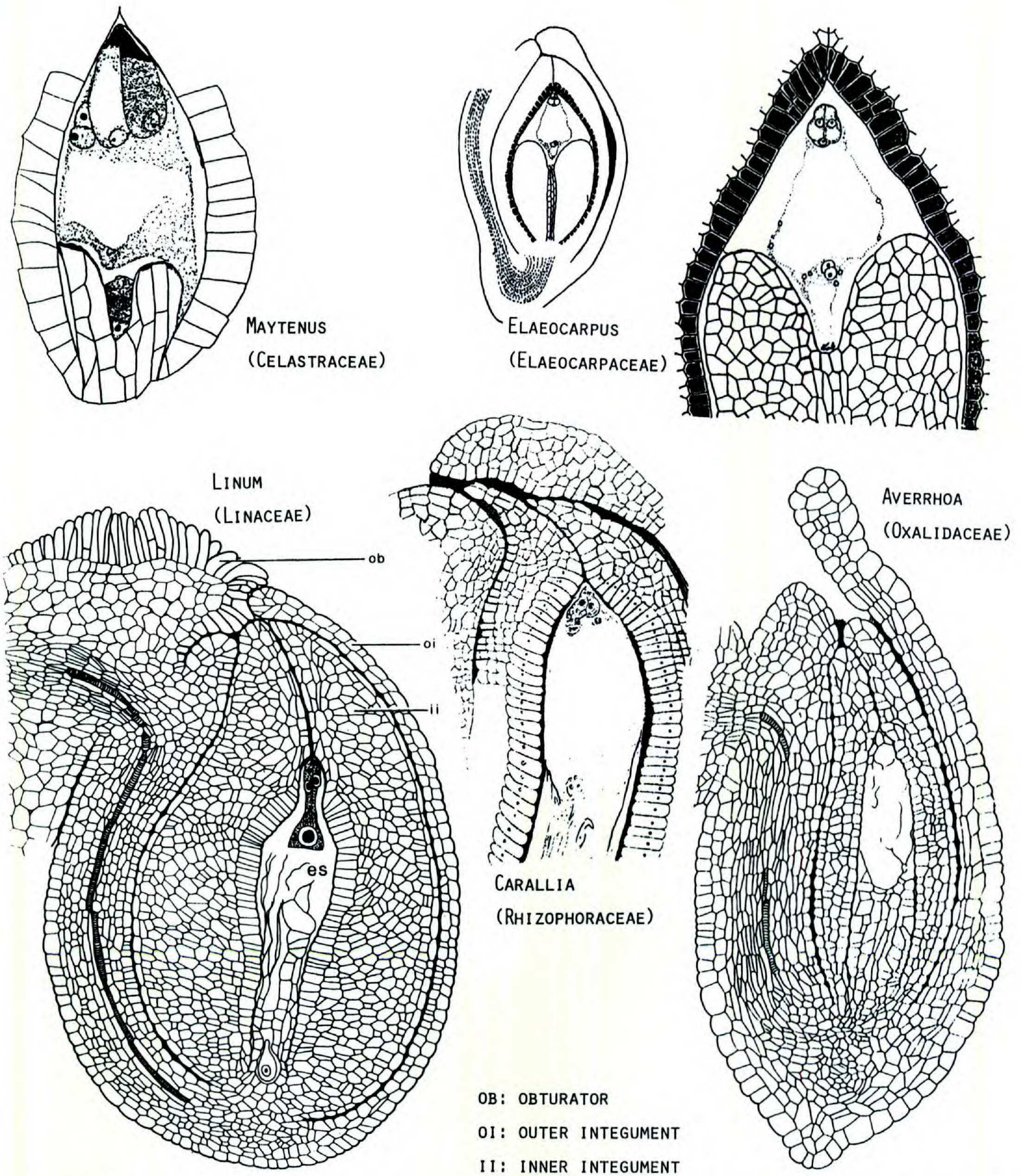


FIGURE 1. Comparison of anatropous bitegmic ovules in several families having an endothelium lining the embryo sac. All have nuclear endosperm formation. *Maytenus* from Andersson (1931), *Elaeocarpus* from Venkata Rao (1953), *Linum* from Boesewinkel (1980), *Carallia* from Karsten (1891), and *Averrhoa* from Boesewinkel (1985).

erties, that family is likely to be closely related to Rhizophoraceae.

#### “RHIZOPHORACEOUS” CHARACTER CONDITIONS

For the following properties, most emphasis has been laid on families that are realistic as potentially related to the Rhizophoraceae. For example, mono-

cotyledons, most sympetalous dicotyledons, taxa of Magnoliiflorae, Ranunculiflorae, Caryophylliflorae, and others have largely been ignored.

1. *Presence of endothelium.* Occurrence of endothelium (integumentary tapetum) was surveyed by Kapil & Tiwara (1978). In most groups having endothelium the ovules are unitegmic and



tenuinucellate. These will not be considered here. Groups having a combination of endothelium and bitegmic ovules are shown as follows. They have nuclear (or rarely helobial) endosperm formation and include taxa with crassinucellate as well as tenuinucellate ovules.

### *Endothelium*

#### I. In combination with crassinucellate ovules

Rhizophorales: Rhizophoraceae (Narayana, 1970)

Malvales: Elaeocarpaceae (Mauritzon, 1934; Venkata Rao, 1953)

Geraniales: Erythroxylaceae (Boesewinkel & Geenen, 1980), Linaceae (Boesewinkel, 1985), Oxalidaceae (Boesewinkel, 1985), Zygophyllaceae, Balanitaceae (Narayana, 1957)

Celastrales: Celastraceae (Andersson, 1931)

#### II. In combination with tenuinucellate ovules

Theales: Lecythidaceae, Scytopetalaceae

Ebenales: Ebenaceae

Primulales: Myrsinaceae, Primulaceae

Most Rhizophoraceae probably have endothelium (although vestigial in the Rhizophoreae according to Juncosa, pers. comm.).

Rhizophoraceae were not mentioned by Kapil & Tiwara (1978), and the list thus is likely to be somewhat incomplete.

The endothelium will be further discussed below under the combination of character conditions.

2. *Presence of aril formed from the exostome.* Occurrence of arils is scattered and has restricted significance. Corner (1949, 1976) tended to regard the presence of arils as an archaic feature, while most other botanists seem to consider them polyphyletic and of rather recent origin. Arils comprise histologically diverse structures and are thus undoubtedly polyphyletic. However, it is likely that arils have developed early in some groups and then have been reduced or lost in some of their derivatives, e.g., in combination with fruit evolution from capsules to berries or drupes. Occasional presence of arils, as in Rhizophoraceae, thus could be considered potentially useful and a possibly plesiomorphic character state.

What is of primary interest here is the occurrence of *exostomal arils*, as this is the kind present in Rhizophoraceae. Such arils occur at least in the following taxa:

Rhizophorales: Rhizophoraceae *pro parte* (at least 4 genera of tribe Macarisieae)

Malvales: Elaeocarpaceae: *Peripentadenia* (Hyland & Coode, 1982)

Celastrales: Celastraceae (common; see Andersson, 1931)

Theales: Clusiaceae *pro parte* (at least in *Clusia*)

Rutales: Meliaceae *pro parte* (at least in *Apanomixis*)

[Geraniales: Erythroxylaceae: *Aneulophus* (dubiously)]

Arils present in various other groups such as genera of Elaeocarpaceae (Malvales), Lepidobotryaceae (Geraniales), Gonystylidaceae (Thymelaeales), Connaraceae and Sapindaceae (Sapindales), Clusiaceae (Theales), and Rutaceae and Meliaceae (Rutales) according to Corner (1976) are mostly or wholly formed from the chalaza or raphe, or both. More studies are needed to clear up homology conditions for using aril structures.

3. *Seed coat with fibrous exotegmen.* According to Corner (1976), a fibrous exotegmen occurs in the following taxa:

Rhizophorales: Rhizophoraceae *pro parte*; probably all genera except the Rhizophoreae and *Carallia* of Gynotrocheae (Juncosa, pers. comm.).

Malvales: Elaeocarpaceae

Geraniales: Erythroxylaceae, Ixonanthaceae, Linaceae, Humiriaceae, and Oxalidaceae

Celastrales: Celastraceae

Euphorbiales: Euphorbiaceae: Phyllanthoideae

Sapindales: Connaraceae, Sapindaceae *pro parte*, and Staphyleaceae *pro parte*

Myrtales: Combretaceae, Lythraceae (including Punicaceae and Sonneratiaceae), and Onagraceae

Others: Aristolochiaceae, Cappariaceae, Caricaceae, Flacourtiaceae, Malpighiaceae, Violaceae, and additional families

Corner (1976) commented on *Gynotroches* and *Pellacalyx* (of his Legnotidaceae) that the exotegminal cells are long and sclerotic. This condition could represent the ancestral type in Rhizophoraceae and must be considered potentially useful in phylogenetic considerations (see Juncosa, 1984a).

Further notes on the seed coat will be given below.

4. *Chlorophyllous embryo.* The embryo in Rhizophoraceae is always or at least generally chlorophyllous (Schimper, 1892; Cronquist, 1981). A chlorophyllous embryo is often found in exendospermous seeds, a tendency that is marked in



monocotyledons but not as clear in dicotyledons; for instance, the seeds are endospermous in Rhizophoraceae.

Yakovlev & Zhukova (1980) and Dahlgren (1980b) have respectively listed and commented on the distribution of chlorophyllous embryos in seeds. In choripetalous dicotyledons their distribution is as follows (mainly according to Yakovlev & Zhukova, 1980):

Rhizophorales: Rhizophoraceae (all or most species; not included by Yakovlev & Zhukova)

Malvales: virtually all families: Bombacaceae, Cistaceae, Dipterocarpaceae, Elaeocarpaceae, Malvaceae (most taxa), Sterculiaceae, and Tiliaceae

Celastrales: Celastraceae

Geraniales: virtually all families, including Erythroxyloxyaceae, Geraniaceae, Linaceae, Oxalidaceae, and Zygophyllaceae

Sapindales: various families, e.g., Aceraceae, Anacardiaceae, Hippocastanaceae, Sapindaceae, and Staphyleaceae

Rutales: most families, among them, Burseraceae, Meliaceae, Rutaceae, and Simaroubaceae

Polygalales: Polygalaceae

Rhamnales: Rhamnaceae

Fabales: all

Theales: Clusiaceae

Other groups: including scattered families of Myrtales; many Capparales, especially Brassicaceae; many Nymphaeales; many Caryophyllales; all Salicales; many Euphorbiales; many Santalales; Plumbaginales; and some taxa in Violales (Violaceae) and Cornales (Icacinaceae, Alangiaceae, Cornaceae)

This character previously has been quite overlooked in phylogenetic considerations.

5. *Sieve-tube plastids with numerous, variably large, square or polygonal protein bodies.* This type of protein has been found by Behnke (1982, 1984) in all genera of Rhizophoraceae studied (see above), *Erythroxyloxy* (Erythroxyloxyaceae, Geraniales), and *Cyrilla* (Cyrillaceae, Ericales). In the last-mentioned family the sieve-tube plastids also contain thin protein filaments.

Cyrillaceae are so different from Rhizophoraceae in overall characters that they can probably be dismissed from consideration as closely related.

Of other families with different shapes and numbers of protein bodies in the sieve tubes may be mentioned Oxalidaceae (including *Averrhoa*), Con-

naraceae, Eucryphiaceae, and Vitaceae (Behnke, 1981).

The presence of the same type of protein configurations in Rhizophoraceae and Erythroxyloxyaceae is of interest in light of a number of other similarities between the two families. If this type represents a synapomorphy of these two families, this would indicate a *very* close relationship (a sister group relationship). As will be commented on below under Erythroxyloxyaceae, there is not sufficient evidence for that.

6. *Presence of certain types of alkaloids.* Rhizophoraceae contain three types of alkaloids (see Hegnauer, 1973): pyrrolidine, tropine, and pyrrolizidine alkaloids.

Hygroline, an alcohol of hygrine, is a *pyrrolidine alkaloid*. It is known in species of *Carallia* (Fitzgerald, 1965) and *Gynotroches* (Johns et al., 1967) of Rhizophoraceae, in at least two species of *Erythroxyloxy* of Erythroxyloxyaceae, and in *Cochlearia* of Brassicaceae. Hygrine is also known in Convolvulaceae, Solanaceae, and Orchidaceae (Gibbs, 1974).

Of other pyrrolidine alkaloids, gerrardamine, gerrardine, and gerrardoline are known in *Cassipourea gerrardii* of Rhizophoraceae but not in other taxa (Gibbs, 1974). Pyrrolidine alkaloids are otherwise rather scattered in angiosperm families.

Tropane alkaloids, surveyed by Romeike (1978) are known in the following groups:

Rhizophorales: Rhizophoraceae (*Bruguiera*)  
(Loder & Russel, 1966)

Malvales: Elaeocarpaceae (*Peripentadenia*)  
(Johns et al., 1971)

Geraniales: Erythroxyloxyaceae (*Erythroxyloxy*)

Euphorbiales: Euphorbiaceae (*Phyllanthus*)

Other groups: Solanaceae (numerous genera),  
Convolvulaceae, Brassicaceae, Proteaceae,  
Dioscoreaceae, and Orchidaceae

*Bruguiera* contains a few tropane alkaloids. Some, like brugine, are unique to *Bruguiera*; others are shared between *Bruguiera* and either of *Dyboisia* (Solanaceae) or *Erythroxyloxy* (Erythroxyloxyaceae). *Peripentadenia* (Elaeocarpaceae) contains tropacocaine, as does *Erythroxyloxy*.

Pyrrolizidine alkaloids, surveyed by Culvenor (1978), are represented by cassipourine, a 1-aminopyrrolizidine derivative, in *Cassipourea* of Rhizophoraceae. Pyrrolizidine alkaloids are scattered in angiosperms and are known in the following groups (Culvenor, 1978; Seigler, 1977):



Rhizophorales: Rhizophoraceae (*Cassipourea*; Bull et al., 1968)

Malvales: Elaeocarpaceae (*Aristotelia*) (Bick et al., 1971)

Celastrales: Celastraceae (*Bhesa*)

Euphorbiales: Euphorbiaceae (*Phyllanthus*, *Securinega*)

Ebenales: Sapotaceae (*Mimusops*, *Planchonella*)

Santalales: Santalaceae (*Thesium*)

Other groups: Apocynaceae, Scrophulariaceae, Asteraceae (many genera), Ranunculaceae, Fabaceae, Boraginaceae (many genera), Poaceae, and Orchidaceae

It is difficult to judge the significance of these three alkaloids. According to Hegnauer (1973), they are all derived from the amino acid ornithine. A shared inherent ability to synthesize such alkaloids in taxa of Rhizophoraceae, Elaeocarpaceae, Celastraceae, and Erythroxylaceae (perhaps also some Euphorbiaceae: Phyllanthoideae) based on a common ancestry should be considered.

#### COMBINED OCCURRENCE OF EMBRYOLOGICAL AND SEED CHARACTERS

The following combination of character conditions is found in Rhizophoraceae. Its occurrence in other families will be considered particularly significant here in the evaluation of the closest relationships of the family.

1. Ovules anatropous (to hemianatropous).
2. Ovules bitegminal, with a micropyle tending to be zigzag.
3. Inner integument three- to several-layered.
4. Ovules modestly to weakly crassinucellate.
5. Parietal cell cut off from primary archesporial cell, dividing a few times.
6. Nucellus lateral to embryo sac disintegrating at an early stage.
7. Inner integument forming an integumentary tapetum of  $\pm$  palisadelike cells (an endothelium).
8. Endosperm formation nuclear.
9. Endosperm retained and  $\pm$  copious in the ripe seed.
10. Embryo of the ripe seed chlorophyllous.
11. Seed coat exotegminal, exotegmen fibrous.
12. Aril tending to be present, exostomal.

The first eleven states are found in the following groups:

Rhizophorales: Rhizophoraceae *pro parte*  
Malvales: Elaeocarpaceae

Celastrales: Celastraceae

Geraniales: Erythroxylaceae, Humiriaceae, Linaceae, and Oxalidaceae

Exostomal arils, additionally, are found at least in Celastraceae. Apart from these families, certain other not yet sufficiently investigated minor families, e.g., Lepidobotryaceae of Geraniales, are likely to agree with these groups mentioned. Also, members of Theales (e.g., Clusiaceae), Euphorbiales (members of Phyllanthoideae, Dichapetalaceae), Thymelaeales (Gonystylaceae), and others agree in some of these characters and cannot be wholly excluded from consideration as potentially close relatives of Rhizophoraceae.

As regards alkaloids, it is also obvious that families like Elaeocarpaceae, Erythroxylaceae, and Celastraceae show similarity to Rhizophoraceae, supporting (rather than being neutral or contradictory to) the embryological evidence.

#### CONCLUSIONS

Having used a limited number of characters to select families that qualify as more or less closely related to Rhizophoraceae, each of the following families and orders will be briefly compared with this family with respect to all-around similarity.

1. Elaeocarpaceae, which are presumably incorrectly placed in Malvales.
2. Celastraceae (including Hippocrateaceae), which are generally placed in their own order Celastrales, often along with various minor and insufficiently known families.
3. Erythroxylaceae of Geraniales; their position in this order has never been questioned in recent years and they also agree well with other Geraniales (or Linales) such as Hugoniaceae, Linaceae, and Oxalidaceae.
4. Lepidobotryaceae and Ctenolophonaceae, two unigeneric families of Geraniales, which are unknown in practically all of the respects considered above but which in general morphology approach Rhizophoraceae tribe Macarisieae.
5. Other taxa of Geraniales.
6. Certain other groups of Theales, Ebenales, Sapindales, and Rutales.
7. The order Myrtales.

#### FAMILIES PUTATIVELY RELATED TO RHIZOPHORACEAE

1. *Elaeocarpaceae*. This family, with about 10 genera and 400 species, is usually placed at the "bottom" of the Malvales near Tiliaceae. In various systems, e.g., that of Hutchinson (1959),



and some textbooks (Davis, 1966; Hegnauer, 1973), Elaeocarpaceae are even included in Tiliaceae. The absence of mucilage cells and cavities, stellate hairs, nectar hairs at the calyx base, and of fatty acids with a cyclopropenyl ring, in combination with the presence of imbricate sepals, a nectariferous disc at the base of the stamens, endothelium, and other features are all foreign to other Malvales and justify their exclusion from that order.

Elaeocarpaceae and Rhizophoraceae are woody, and in wood anatomy Elaeocarpaceae are more advanced than most Rhizophoraceae, having, as a rule, vessel members with simple perforations. Wood rays are heterogeneous, mixed uniseriate and pluriseriate, as in Rhizophoraceae. The parenchyma is usually paratracheal and very sparse (different from most primitive Rhizophoraceae); mucilage canals and cavities are present.

The nodes are trilacunar, as in Rhizophoraceae. The leaves are often alternate in Elaeocarpaceae. As in Rhizophoraceae, stipules are present; they may be persistent or caducous. The leaf venation is at least partly brochidodromous, as in some Rhizophoraceae, but sometimes eucamptodromous, although Hickey & Wolfe (1975) attributed Malvales in general with actinodromous venation. Furthermore, the leaf teeth in Elaeocarpaceae according to Hickey & Wolfe (1975) are mainly of the violoid type, this resembling the theoid type, which these authors reported for Celastraceae. The teeth in Elaeocarpaceae are obviously more or less different, however, from the peculiar macarisioid teeth in Rhizophoraceae (Keating & Randrianasolo, this volume). Stomata in Elaeocarpaceae are paracytic to cyclocytic and are restricted to the lower leaf surface, as in Rhizophoraceae. Crystals are present in the parenchyma and are generally solitary and prismatic, as are the crystals in Rhizophoraceae tribe Macarisieae. The hairs, when present, are simple and unicellular, as in Rhizophoraceae.

Likewise matching this family, the inflorescences are mostly axillary cymes or panicles, and the flowers are hypogynous and probably primitively pentamerous. The sepals are valvate to imbricate, and the petals are distinct (rarely basally connate) and frequently distally lobate or fimbriate, as in most nonmangrove Rhizophoraceae. A more or less conspicuous disc is present (Balgooy, 1982), as in nearly all Rhizophoraceae. The stamens are 1–3 times the petal number or usually more (van Heel, 1966), the diplostemonous condition being probably plesiomorphic. Haplostemony, as in Celastraceae, is found within *Sloanea*. Both in the basic

state and in the increase of stamens, Elaeocarpaceae agree with Rhizophoraceae. The stamens have narrow filaments, as in Rhizophoraceae tribe Macarisieae, but the anthers are advanced, having at least in some genera a nonfibrous endothecium and, as a rule, apical dehiscence by short slits or pores.

The two families largely agree in pollen morphology, the pollen grains being mostly tricolporate, with rather thick exine and a rugulate-punctate surface. They are dispersed in the two-celled state in both families.

Carpel number is variable, as in Rhizophoraceae; the carpels are fused in the styler region, the style being simple or apically lobate. The ovary is two- to several-loculed with axile placentation, in which the Elaeocarpaceae agree with Rhizophoraceae. As pointed out above under Rhizophoraceous Character Conditions, embryology in Elaeocarpaceae is essentially similar to that in Rhizophoraceae, although the arils when present in the former (according to Corner, 1976) are not exostomal but developed from the chalaza and raphe.

The fruit in Elaeocarpaceae is a capsule or drupe. The seeds have copious endosperm, with fat oils and protein and a chlorophyllous embryo, all the conditions in Rhizophoraceae. Arillate seeds occur in some species, and the aril in *Peripentadenia* is reportedly “a total covering of thick flesh outgrown from the distal cap” (Hyland & Coode, 1982).

Elaeocarpaceae agree with Rhizophoraceae in alkaloid chemistry (see above) and both are tannin plants. Ellagic acid is (rarely) present in both families. Both produce proanthocyanins as well as caffeic acid, and in both the flavonoids include myricetin, quercetin/kaempferol, and pelargonidin (Gornall et al., 1979). In fact, Elaeocarpaceae agree much better with regard to their secondary metabolites with Rhizophoraceae than with Tiliaceae, with which they are generally associated.

Briefly, the Elaeocarpaceae differ from the Rhizophoraceae mainly in some wood-anatomical details, in having usually alternate leaves and different anther morphology, and in basic chromosome number. Furthermore, the sieve-tube plastids accumulate starch, not protein. The floral receptacle is rarely as well developed as in Rhizophoraceae. Arils, when present, may be of different origin.

This supports the following conclusions: 1. Elaeocarpaceae make up a distinct family. 2. They are misplaced in Malvales. 3. They are closely related to Rhizophoraceae.

2. *Celastraceae*. Celastraceae comprise a fairly large family of roughly 50 genera and 800 species (Cronquist, 1981). The family is variable



and somewhat difficult to define. All members are woody plants. Secretory canals ("laticifers") are often present in phloem of stem and leaves; this is also a feature met with in Rhizophoraceae (see, for example, Keating, 1984). Contrary to Rhizophoraceae, the Celastraceae are said to have unilacunar nodes. Vessel perforation is simple or rarely scalariform; variation is great in wood rays and wood parenchyma. Oxalate crystals of simple, prismatic type and as crystal druses (also crystal sand) occur in Celastraceae as well as in Rhizophoraceae. The leaves are opposite or alternate and simple and generally have small and/or caducous stipules or none at all (the stipules are generally larger in Rhizophoraceae). The venation is pinnate-brochidromous with apically elongated arches; lateral teeth, where present, are of the theoid type (Hickey & Wolfe, 1975), agreeing probably more with Elaeocarpaceae than with Rhizophoraceae.

Hairs are infrequent and short and unicellular when present (Metcalf & Chalk, 1950), as in Rhizophoraceae; in both families the stomata are generally confined to the lower surface of the leaves. In the Celastraceae they are anisocytic or anomocytic, only rarely paracytic, and thus mostly different from those in Rhizophoraceae.

The inflorescences in the Celastraceae and Rhizophoraceae are frequently axillary cymes or panicles (or solitary). The flowers are generally small and greenish, regular, 4–5-merous, and hypogynous, perigynous, or half-epigynous. In these respects the Celastraceae largely agree with Rhizophoraceae. However, the sepals are less developed and valvate to imbricate, the petals are often roundish, and the disc in most cases is more conspicuous and often square or 5-angular. The petals in Celastraceae to my knowledge are never fimbriate or lacinate apically, as is usual with Rhizophoraceae. Further, the androecium is restricted to a single alternipetalous whorl, although clearly derived from a diplostemonous condition (alternisepalous staminodes occur in *Lophopyxis*).

The pollen grains are mostly tricolporate, with sexine thicker than nexine, simplibaculate (Erdtman, 1952), and basically agree with the pollen in Rhizophoraceae. They are two- or three-celled when dispersed (Brewbaker, 1967).

The pistil consists of 2–5 carpels and has a single terminal style with capitate or lobate stigma. Each of the 2–5 locules contains as a rule two axile ovules. In these respects, as in nearly every detail of the embryology, the Celastraceae agree with the Rhizophoraceae tribe Macarisieae, including presence of endothelium, exostomal aril, and exotegminal, fibrous seed coat. The seeds have a chlorophyllous embryo.

The Celastraceae show a much wider chemical spectrum than Rhizophoraceae and Elaeocarpaceae but agree in being essentially tannin plants. They produce proanthocyanins and caffeic acid; ellagic acid has been reported in some individual species. Furthermore, the flavonoid spectrum agrees (Hegnauer, 1964) with the mentioned two families in presence of quercetin, kaempferol, myricetin, and other flavonoids. A pyrrolizidine alkaloid has been reported (see above), the significance of which is, however, uncertain. On the other hand, Celastraceae generally produce saponins (Bossert & Pernet, 1957) and often alkaloid amines, e.g., cathine (Cronquist, 1981), which are unknown in Rhizophoraceae and Elaeocarpaceae.

Besides other basic chromosome numbers,  $x = 8$  is known in Celastraceae, as in some Rhizophoraceae.

Celastraceae obviously agree well with the Rhizophoraceae in essential characters but can be considered more derived in the haplostemonous flowers with little-developed calyx and generally massive disc. Further, they have the ability to produce saponins and certain amines and differ with regard to sieve-tube plastid inclusions. They form a more heterogeneous assemblage, with some genera having spread to temperate climates.

3. *Erythroxylaceae*. Erythroxylaceae consist of only the genera *Erythroxylon*, *Nectaropetalum*, *Pinacopodium*, and *Aneulophus*, the last often placed in Linaceae. *Erythroxylon* consists of ca. 200 species; the other genera are small. Erythroxylaceae are placed in Geraniales (or Linales) near Linaceae and Humiriaceae in all current classifications, and a number of shared features support this. Nevertheless, Erythroxylaceae (as well as some other families of Geraniales) agree with the Rhizophoraceae in several conspicuous features, warranting a close comparison between the two families.

Like the Rhizophoraceae, all Erythroxylaceae are woody but generally shrubby. The vessels have simple perforations in the end walls, a conspicuous difference from most Rhizophoraceae, but the wood rays are mostly heterocellular, mixed uni- and pluriseriate, as in that family. Essential oils are sometimes found in the wood.

A highly conspicuous similarity between Rhizophoraceae and Erythroxylaceae is the similar kind of protein bodies of the sieve-tube plastids (see above).

The leaves are alternate or rarely (*Aneulophus*) opposite and have brochidromous venation of the secondary veins (Hickey & Wolfe, 1975), agreeing in this rather well with various Rhizopho-



raceae. Their teeth are mostly of the theoid type. Stipules are present, as in Rhizophoraceae; they are intrapetiolar and often tricuspidate. The stomata are paracytic and generally restricted to the lower surface of the leaves. Sclereids are sometimes present, while this in Rhizophoraceae is mainly the case with mangrove genera (tribe Rhizophoreae). Hairs are simple and unicellular when present. Solitary crystals of oxalate are found in some tissues.

The inflorescences are axillary panicles or cymes or consist of solitary flowers, as in Rhizophoraceae. A peculiarity of the Erythroxyllaceae is that the axis of these inflorescences often bears a great number of bracteate leaves (raments, cataphylls). The flowers are small, actinomorphic, pentamerous in perianth and androecium, and hypogynous. The sepals are valvate or imbricate and basally connate. The petals are entire (not fimbriate or laciniate), free from each other, and usually adaxially appendaged. Unlike most Rhizophoraceae, Elaeocarpaceae, and Celastraceae, disc structures are lacking. The androecium is diplostemonous; the ten stamens are situated in a single whorl and the bases of their filaments are usually connate into a short tube. The anthers are tetrasporangiate, longitudinally dehiscent, and extrorse.

The pollen grains, as in most Rhizophoraceae, are tricolporate, with rather thick exine and often with a reticulate surface. They are, however, three-celled, whereas those in Rhizophoraceae are two-celled.

The pistil is 2–4-carpellary, with (2–)3(–4) locules and usually with 3 separate stylodia, each with a more or less expanded, often capitate stigma; sometimes, as in *Nectaropetalum*, there is a single, apically bilobate style (Verdcourt, 1981). Each locule contains one (or two) axillary and pendulous ovule(s); only one ovule usually develops in each fruit. The embryological characters are essentially as in Rhizophoraceae (see above). The fruit is generally a drupe, the single seed of which usually has copious endosperm (with starch) but may lack endosperm. Arils are lacking, except in *Aneulophus*, but the nature of the aril in this genus is uncertain, possibly exostomal (see Wilczek, 1958).

The chemical conditions are somewhat similar to those in Rhizophoraceae as regards alkaloids (tropane alkaloids—cocaine, for instance—are present and sometimes copious) and tannins; however, saponins, cyanogenic compounds, and ethereal oils are sometimes present, which is obviously not the case in Rhizophoraceae.

The basic chromosome number,  $x = 12$ , deviates from Rhizophoraceae.

Accordingly, Erythroxyllaceae and Rhizophora-

ceae exhibit important differences and important similarities. The flowers in Erythroxyllaceae lack a floral disc, in contrast with most Rhizophoraceae (but it is absent from *Pellacalyx* of this family). In Erythroxyllaceae the floral receptacle is much less developed and never cupular, cataphyllous leaves are common (but probably evolved within Erythroxyllaceae), and the pollen grains are three-celled.

Erythroxyllaceae agree well with other Geraniales in most respects; in fact there are difficulties in delimiting them from, for example, Linaceae (*Aneulophus* and *Nectaropetalum* having been referred to both families). This is no argument against considering Rhizophoraceae (as well as Elaeocarpaceae and Celastraceae) as closely related to Erythroxyllaceae and other families of Geraniales.

The following conclusions are drawn from the evidence presented here:

1. There are no arguments to exclude Erythroxyllaceae from Geraniales (or from Linales, if this order is separated from Geraniales, as by Cronquist, 1981).

2. The Erythroxyllaceae show numerous and essential similarities to Rhizophoraceae, which together support that they are relatively closely related.

3. This similarity is, however, not as far-reaching as that between Rhizophoraceae and Elaeocarpaceae, and there is not sufficient evidence that Rhizophoraceae and Erythroxyllaceae can be “sister groups” in the phylogenetic sense.

4. Therefore, it is most likely that the very particular kind of sieve-tube plastids that the two families have in common has evolved by convergent evolution in the ancestors of each of the two families. (An alternative is that a certain disposition for them evolved in a common ancestor, although this is concealed or blocked in other related families.)

4. *Lepidobotryaceae*, *Ctenolophonaceae*. *Lepidobotryaceae* are often included in either Oxalidaceae or Linaceae. They may be circumscribed so as to include either only *Lepidobotrys* Engl. or also *Sarcotheca* Blume and *Dapania* Korth. *Lepidobotrys* occurs in Africa, *Sarcotheca* in Malaysia, and *Dapania* in Malaysia and Madagascar.

The present comments will be restricted to *Lepidobotrys* (see Leonard, 1950, 1958) without evaluating the circumscription of the family.

*Lepidobotrys* is a tree with alternate leaves, which have small stipules and one large leaf lamina; somewhat below this the petiole has a “joint” at which is situated a much smaller sheathing leaflet, often called a “stipel.” The anatomical features



remain insufficiently known, but according to Metcalfe & Chalk (1950), the vessels have scalariform perforation plates, and the intervacular pitting is minute and alternate.

Wood parenchyma is abundant and consists of scattered cells containing oxalate crystals. The rays are almost exclusively uniseriate and almost homogeneous (Metcalfe & Chalk, 1950). The inflorescences are small, axillary and racemelike; their axis bears densely set scales, in the axils of which the flowers are situated. Young inflorescences therefore are conelike. The flowers are fairly long-pedicelled, actinomorphic, mainly pentamerous, diplostemonous, functionally unisexual, and tricarpeal. The petals are imbricate, and the mutually free filaments of the 10 stamens are inserted on a lobate, well-developed disc. The pollen grains are tricolporate with reticulate exine (see Oltmann, 1971). The pistil is trilocular and has three free, apically bilobate stylodia. The functionally male and female flowers differ in having either well-developed stamens and rudimentary (but distinctive) pistil or smaller, nonfunctional stamens and a well-developed pistil. Each locule possesses two apical-axile ovules. The embryology is unknown. The fruit is a one-seeded capsule with a funicular aril.

This genus has a floral structure similar to that in certain species of Rhizophoraceae tribe Macariseae, although in stylar conditions it more resembles Anisophylleaceae. It is an example of some rather isolated genera in Geraniales that have been variously treated as separate families or included in Oxalidaceae or Linaceae.

Another isolated genus, *Ctenolophon*, is sometimes treated as the separate family Ctenolophonaceae and is sometimes included in Linaceae. This genus has opposite, stipulate leaves, as in Rhizophoraceae, and a panicle of pentamerous, diplostemonous flowers with a prominent disc and a bilocular pistil with a single style, all known in Rhizophoraceae. The pollen grains are extraordinarily different, however (see, for example, Erdtman, 1952; Oltmann, 1971). The fruit is a nutlet with a single arillate seed. The nature of the aril is not quite clear. *Lepidobotrys* and *Ctenolophon* are mentioned here as a complement to Erythroxylaceae, as they are currently considered good members of Geraniales (or Linales) yet resemble the Rhizophoraceae in some respects in which the Erythroxylaceae differ from the Rhizophoraceae; *Lepidobotrys* in the more enlarged floral axis with a prominent, somewhat lobate disc and in the free filaments, a floral structure clearly similar to that in, for example, *Gynotroches*; *Ctenolophon* in the

opposite leaves, distinct floral disc, separate filaments, and single (although apically bibrachiate) style.

5. *Other Geraniales.* Whereas it seems as if the Rhizophoraceae show closest similarity to Erythroxylaceae and certain variously placed genera such as *Lepidobotrys* and *Ctenolophon*, which deserve further embryological, anatomical, and chemical studies, there is also, as noted above, great embryological similarity with Linaceae, Oxalidaceae, and Balanitaceae. Woody members of the first of these families and of Balanitaceae, Humiriaceae, Hugoniaceae, and Zygophyllaceae need be considered as potentially closely related to Rhizophoraceae.

6. *Members of Theales, Ebenales, Sapindales, and Rutales.* It has been stated above that several character states of the above-mentioned combination of embryological attributes occur in other groups, mainly of these four orders.

The Theales are variously circumscribed, with Lecythidaceae included or not. Within this complex in the wide sense, endothelium is reported for Lecythidaceae and may well occur in other families; an exostomal aril is found in at least some species of *Clusia*, of Clusiaceae; within this family the embryo may also be chlorophyllous. Sapotaceae in the probably highly heterogeneous order Ebenales show quite a number of similarities to Rhizophoraceae (and various Theales). Presumably primitive Theales and, separately, primitive Malvales evolved from ancestors with rather simple tetra- or pentamerous, diplostemonous flowers; in each of the Theales and Malvales lines an increase in stamen number seems to have occurred. Such an increase of stamen number can also be observed *within* each of Rhizophoraceae and Elaeocarpaceae. It is probable that other evolutionary lines evolved from groups with such simple, diplostemonous flowers, e.g., Geraniales, Sapindales, and Rutales, each line retaining some of the plesiomorphies while developing its own specializations (autapomorphies).

7. *The Myrtales.* Myrtales also most likely evolved from an ancestor with penta- or tetramerous, actinomorphic, hypogynous, diplostemonous flowers with a disc (see Dahlgren & Thorne, 1984). The Myrtales are less specialized in embryological characters than the Rhizophoraceae, having a more persistently multicellular nucellus and no endothelium (Tobe & Raven, 1983) and having nonchlorophyllous embryo and exendospermous seeds. The



nodes in Rhizophoraceae are trilacunar, which is extremely rare in Myrtales (found only in *Alzatea*). Vessels in Rhizophoraceae are more primitive than those in Myrtales in having scalariform perforation plates. The alkaloid chemistry in Rhizophoraceae has no correspondence in Myrtales. Finally, Rhizophoraceae lack internal phloem and vestured pits. This evidence all supports the view held at the Myrtales symposium (see, for example, Dahlgren & Thorne, 1984) that Rhizophoraceae are not closely related with Myrtales.

For Anisophylleaceae, earlier included in Rhizophoraceae, most of these objections against a close relationship to Myrtales are lacking (although some others may be added, as lack of stipules).

#### MONOPHYLY AND CHARACTERIZATION OF ANISOPHYLLEACEAE

Anisophylleaceae consists of the genera *Anisophyllea* R. Br., *Combretocarpus* Hook. fil., *Poga* Pierre, and *Polygonanthus* Ducke.

Anisophylleaceae are trees and shrubs, sometimes of considerable size. Characteristic wood anatomical features according to van Vliet (1976) are the simple perforations in the vessels, fibers with distinctly bordered pits, very broad (up to 30 cells wide) multiseriate rays, and the half-bordered, alternate vessel-parenchyma pits. These character states do not distinguish the family absolutely and sharply from Rhizophoraceae; rather the variable Rhizophoraceae with the genera of the tribe Gynotrocheae, in particular *Carallia*, join up with the Anisophylleaceae. As regards vessel diameter, van Vliet (1976) showed that the Anisophylleaceae normally have higher values than Rhizophoraceae (Anisophylleaceae: tangential diameter mostly 160–340  $\mu\text{m}$ , radial diameter to 370–420  $\mu\text{m}$ ; Rhizophoraceae: tangential diameter mostly 40–200  $\mu\text{m}$ , tangential diameter mostly to 85–340  $\mu\text{m}$ ). As other character conditions argue against a close relationship between Rhizophoraceae and Anisophylleaceae, it is not adequate to discuss the wood anatomical “limits” between the families—*Carallia* and other Gynotrocheae are not really intermediate between other Rhizophoraceae and Anisophylleaceae; they are only extreme in the former family. Lysigenous secretory cavities are present in *Poga* (Metcalf & Chalk, 1950).

The leaves in Anisophylleaceae are alternate, simple, entire, and exstipulate. According to Keating & Randrianasolo (this volume), the secondary venation in most Anisophylleaceae is transitional between brochidodromous and (basally on the lamina) eucamptodromous, but it is acrodromous in

*Anisophyllea*. No teeth are present. There is marked anisophylly and often strong asymmetry in the leaves of *Anisophyllea*, which are generally two-ranked and strongly horizontally oriented on plagiotropic shoots.

The inflorescences are axillary and generally elongate and catkin- or spikelike.

The flowers are small, usually 4(–5)-merous, but 3-merous in *Combretocarpus* and rarely in *Anisophyllea*; they are actinomorphic, epigynous, diplostemonous, and often unisexual by partial reduction of stamens or pistil (Tobe & Raven, in press). The floral receptacle, which encloses and is fused with the ovary wall, continues as a variably long hypanthium, resembling the condition in many Myrtales.

The petals (see Tobe & Raven, in press) are usually deeply incised, generally with 3, 5, or 7 lobes, which may have an enlarged, glandular tip. These enlarged tips are present in taxa of *Anisophyllea* (*A. laurina*) and *Poga*, and they support these genera as closely related (although they belong to different main branches in the cladogram of Tobe & Raven, this volume). Only *Polygonanthus* has entire petals, although the margin is sometimes finely fimbriate.

Incised to fimbriate petals may represent an autapomorphy of Anisophylleaceae but also occur in most nonmangrove Rhizophoraceae, in most Elaeocarpaceae, in certain genera of each of Diapensiaceae, Primulaceae, Malpighiaceae, and others. The value of this character in connecting Rhizophoraceae and Anisophylleaceae is dubious in the light of the numerous differences. A striking condition, stressed especially by Tobe (pers. comm.), is that the above-mentioned swollen, glandular tips of the petal lobes in Anisophylleaceae are matched in at least *Ceriops* of Rhizophoraceae. However conspicuous this similarity may be, I consider this the result of convergent evolution; Juncosa & Tomlinson (1987) showed that in *Ceriops* these structures are hydathodes.

A lobate intra- and interstaminal, discontinuous disc surrounds the style base. Nectar is produced at the filamental bases. The (6–)8(–10) stamens are incurved in bud and have mutually free, narrow filaments and dorsifixed, ovoid, introrse-latorse anthers (all from Tobe & Raven, in press.)

The pistil ends in (3–)4(–5) separate stylodia. The carpels each form a locule with 1–2 ovules in axile position.

The Anisophylleaceae (Tobe & Raven, in press) show a combination of frequent character conditions, from which there are various exceptions representing further evolutionary developments that



contribute to elucidating the probable evolution within this small family (see cladogram in Tobe & Raven, in press). The endothelium is fibrous, the anther wall formation of the basic type, and the tapetum glandular with 2-nucleate or—by nuclear fusion—1-nucleate tapetal cells.

The pollen grains are tricolporate and, according to Vezey et al. (this volume), have a rather thin tectum with reticulate-punctate surface. Tobe & Raven (1987b) showed that the pollen grains are two-celled when dispersed.

The ovules are bitegmic or (*Anisophyllea* and *Combretocarpus*) unitegmic, with the inner integument in bitegmic ovules only two cells thick, a difference from the Rhizophoraceae; in bitegmic ovules the micropyle is formed by both integuments. The ovules are clearly crassinucellate; the primary archesporial cell cuts off a parietal cell that gives rise to a parietal tissue. The nucellar tissue persists longer than in Rhizophoraceae. No endothelium is formed. Embryo sac formation is of the *Polygonum* type or, in *Combretocarpus*, of the *Allium* type, the latter obviously an autapomorphy for that genus. Endosperm formation is nuclear. The endosperm is used up in the course of seed maturation. The embryo has a long hypocotyl and small to rudimentary cotyledons or no cotyledons at all. The latter conditions are possibly potentially valuable in the search for the relationships of Anisophylleaceae. (Information all according to Tobe & Raven, 1987b.)

Contrary to the Rhizophoraceae and Elaeocarpaceae, the seed coat of the mature seed is not exotegminal-fibrous but consists of the testal epidermis only (exotesta), as in *Poga*, of a multilayered testa (*Polygonanthus*), or of the multilayered or ultimately thin single integument (*Anisophyllea* and *Combretocarpus*, respectively) (Tobe & Raven, this volume). This variation makes difficult comparisons and conclusions on relationships based on seed coat structure.

Chemical information is somewhat incomplete. Aluminium accumulation is highly characteristic (Chenery, 1948), a major difference from Rhizophoraceae but a similarity to various Myrtales. The Anisophylleaceae are clearly tanniniferous plants. Ellagic acid is known in *Anisophyllea* (Lowry, 1968). Alkaloids are unknown.

The above evidence will form the basis for an attempt to evaluate approximate relationships of the Anisophylleaceae, which show no autapomorphy with strong significance comparable to that of the kind of sieve-element plastids in Rhizophoraceae. The homogeneity of Anisophylleaceae therefore rests on the combination of numerous, rather

frequently occurring, and trivial character conditions. These include the similar states of wood characters (see above), accumulation of aluminium, the floral structures (epigyny, tri- or tetramery, presence of hypanthium, generally incised petals, presence of a disc, diplostemony, and separate styloids), and the combination of general embryological characters (see above). Thus, multiple similarities rather than singularity binds together the four genera and support them as a monophyletic unit.

#### RELATIONSHIPS OF ANISOPHYLLEACEAE

Technically the Anisophylleaceae can be defined as follows: woody; vessel perforation simple; leaves alternate, exstipulate, simple, entire; flowers mostly tetramerous, actinomorphic, isomerous in all whorls but diplostemonous, with sepals and petals; filaments free from each other and from the corolla; anthers dehiscing with longitudinal slits; disc present; styloids free; ovules 1–2 per locule, axile, anatropous, crassinucellate, with nuclear endosperm formation; fruit fleshy, indehiscent; seeds exendospermous, with straight embryo.

Such a combination of features is restricted to Anisophylleaceae but may coincide with that in Rosaceae as broadly defined to include Malaceae; however, it is not present in one and the same member of any Rosaceae.

Neglecting tetramery (in all whorls) does not increase the choice, but neglecting also absence of endosperm in the seed, a presumably advanced and recently derived character condition, also adds Flacourtiaceae and Anacardiaceae. Neglecting also the fruit type, the lack of stipules, and the free styloids would bring some Myrtales in agreement with Anisophylleaceae as well, but then the anatomical peculiarities of Myrtales (intraxylary phloem and vested pitting) are not considered either.

Thus, in gross morphology Anisophylleaceae are largely Saxifragalean–Rosalean in nature, and I agree with Cronquist (1981), who placed Anisophylleaceae in Rosales in the broad sense. Also chemical characters agree, largely with those in, for example, Rosaceae in the narrow sense. However, within the Rosales no obvious group agrees particularly well with the Anisophylleaceae, and the alternative families Flacourtiaceae and Anacardiaceae must be considered.

#### FLACOURTIACEAE

Flacourtiaceae comprise a very variable group of often cyanogenic plants with mostly stipulate leaves. Their flowers are nearly always hypogy-



TABLE 2. *Differences between Rhizophoraceae and Anisophylleaceae.*

Character	Rhizophoraceae	Anisophylleaceae
Leaves	opposite	alternate
Stipules	present, interpetiolate	lacking
Vessel perforation	usually scalariform	simple
Vessel diameter	narrow	wider
Sieve element plastids	with particular protein bodies	with starch only
Aluminium accumulation	none	present
Colleters	reported in several genera	none
Inflorescence	pauciflorous, cymules, solitary flower	multiflorous; panicle or panicle-derived
Merism	4-, 5- or > 5-merous	3- or 4-merous
Ovary, style	superior to inferior, a single style	inferior, separate stylobia
Tectum of pollen wall	relatively thick	relatively thin
Subepidermal floral laticifers	present, different types	none
Nucellar tissue	consumed early	persisting longer
Endothelium	present	none
Seeds	endospermous	exendospermous

nous, and the stamens are generally numerous. Furthermore, the ovary generally has parietal placentae. No single genus of Flacourtiaceae to my knowledge has the combination of character condition of the Anisophylleaceae, and it is solely due to the variability (or heterogeneity) of the Flacourtiaceae that it agrees, in most respects, with the Anisophylleaceae.

#### ANACARDIACEAE

Anacardiaceae are members of Sapindales. They are rich in tannins and have well-developed schizogenous or lysigenous ducts or channels with resins, which is not the case with the Anisophylleaceae. The leaves are variable in Anacardiaceae but are more frequently compound than simple, as in Anisophylleaceae. The small flowers are reminiscent of those in Anisophylleaceae but are more often pentamerous; they vary from hypo- or perigynous to epigynous and are often diplostemonous, with free stamens and a well-developed disc. The carpels are often solitary (sometimes several and free from each other) but when fused are generally three. The fruit is usually drupaceous. Anacardiaceae, apart from the resin canals, compound leaves, and numerical conditions of the flower (especially gynoecium), agree fairly well with Anisophylleaceae.

#### CONCLUSION

Anisophylleaceae are difficult to place, as most of their characteristics are of very common occurrence. Rosales(-Saxifragales-Cunoniales) seem to be the group in which they would be fairly well placed, but without obvious links. These orders

have a clearly temperate(-boreal) concentration, which somewhat contrasts with the tropical concentration of Anisophylleaceae. The floral morphological (Tobe & Raven, 1987c) and embryological conditions in Anisophylleaceae agree completely with those common in Rosaceae sensu stricto, for example: exendospermous seeds and a bitegmic, crassinucellate ovule with nuclear endosperm formation. That in both families the ovules are bitegmic in some and unitegmic in other genera is a coincidence. The basic chromosome numbers,  $x = 7$  or  $x = 8$ , are also present in Rosaceae sensu stricto, especially the former number (Raven, 1975).

It is probable that Anisophylleaceae comprise a rather isolated family evolved from ancestors shared between those in Rosales, Cunoniales, and Saxifragales. It is also probable that these were not very remote from the ancestors of Myrtales, although the last order is distinctive in several respects, including the anatomical features mentioned above.

#### PROPOSED CLASSIFICATION

Ordinal composition around Rhizophoraceae:

GERANIALES: Zygophyllaceae, Nitrariaceae, Peganaceae (position uncertain), Balanitaceae, Vivianiaceae, Geraniaceae, Ledocarpaceae, Biebersteiniaceae, Dirachmaceae, Ixonanthaceae, Humiriaceae, Hugoniaceae, Ctenolophonaceae, Erythroxylaceae, Linaceae, Lepidobotryaceae, Oxalidaceae

CELASTRALES: Celastraceae, Elaeocarpaceae, **Rhizophoraceae**



## Ordinal composition around Anisophylleaceae:

CUNONIALES: Cunoniaceae, Baueraceae, Brunelliaceae, Davidsoniaceae, Eucryphiaceae

ROSALES: Crossosomataceae, Rosaceae, Neuradaceae, **Anisophylleaceae**, Malaceae, Amygdalaceae (plus perhaps some smaller families such as Rhabdodendraceae)

SAXIFRAGALES: Saxifragaceae, Penthoraceae, Vahliaceae, Francoaceae, Greyiaceae, Brexiaceae, Grossulariaceae, Iteaceae, Cephalotaceae, Crasulaceae, Podostemaceae.

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